NEW SPECIES OF ACOEL TURBELLARIANS FROM THE PACIFIC COAST

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The acoel turbellarians have been accorded very little attention in North America. Only a few species have been described, and some of these will have to be investigated more completely before their taxonomic position can be established with any degree of certainty. On the Pacific coast, where acoels are abundant in bottom sediments, on algae, and in other situations, apparently only two species have been named. One of these is *Polychoerus carmelensis* Costello and Costello (1938), from central California; the other is *Childia groenlandica* (Levinsen), an acoel which has a wide distribution in North Atlantic waters and which has recently been reported from San Francisco Bay, California (Hyman, 1959).

During the summers of 1961 and 1962, and the autumn of 1964, several species of acoels were taken at various localities on San Juan Island, in the San Juan Archipelago, Washington. Mature individuals of three of these were recovered in sufficiently large numbers to permit a thorough study of their morphology and description as new species. Additional material of one of these acoels was found at Charleston, Coos County, Oregon, during the summer of 1964.

The acoels are a difficult group with which to work. Most of them are small, and certain of their syncytial structures are not sharply delimited. Many published descriptions are incomplete and poorly illustrated. There are even some rather detailed accounts which do not focus sharply on pertinent details, and from which one cannot form a clear picture of the morphology of the acoels concerned. In deciding the taxonomic position of the new species described here, I have relied upon the summary of the genera and higher taxa of acoels given by Westblad (1948).

I wish to express my appreciation to Dr. Robert L. Fernald, Director of the Friday Harbor Laboratories, for many courtesies which facilitated my work.

METHODS

The acoels described in this contribution were for the most part obtained by taking up masses of green algae (*Ulva* and *Enteromorpha*) and washing them by agitation in a pail of sea water. A thin layer of sediment (consisting largely of muddy sand from the substrate) obtained in this way was then distributed in large culture dishes, in water about 2 or 3 cm. deep. Samples of sediment sucked up with a large pipette and examined with a dissecting microscope often contained acoels,

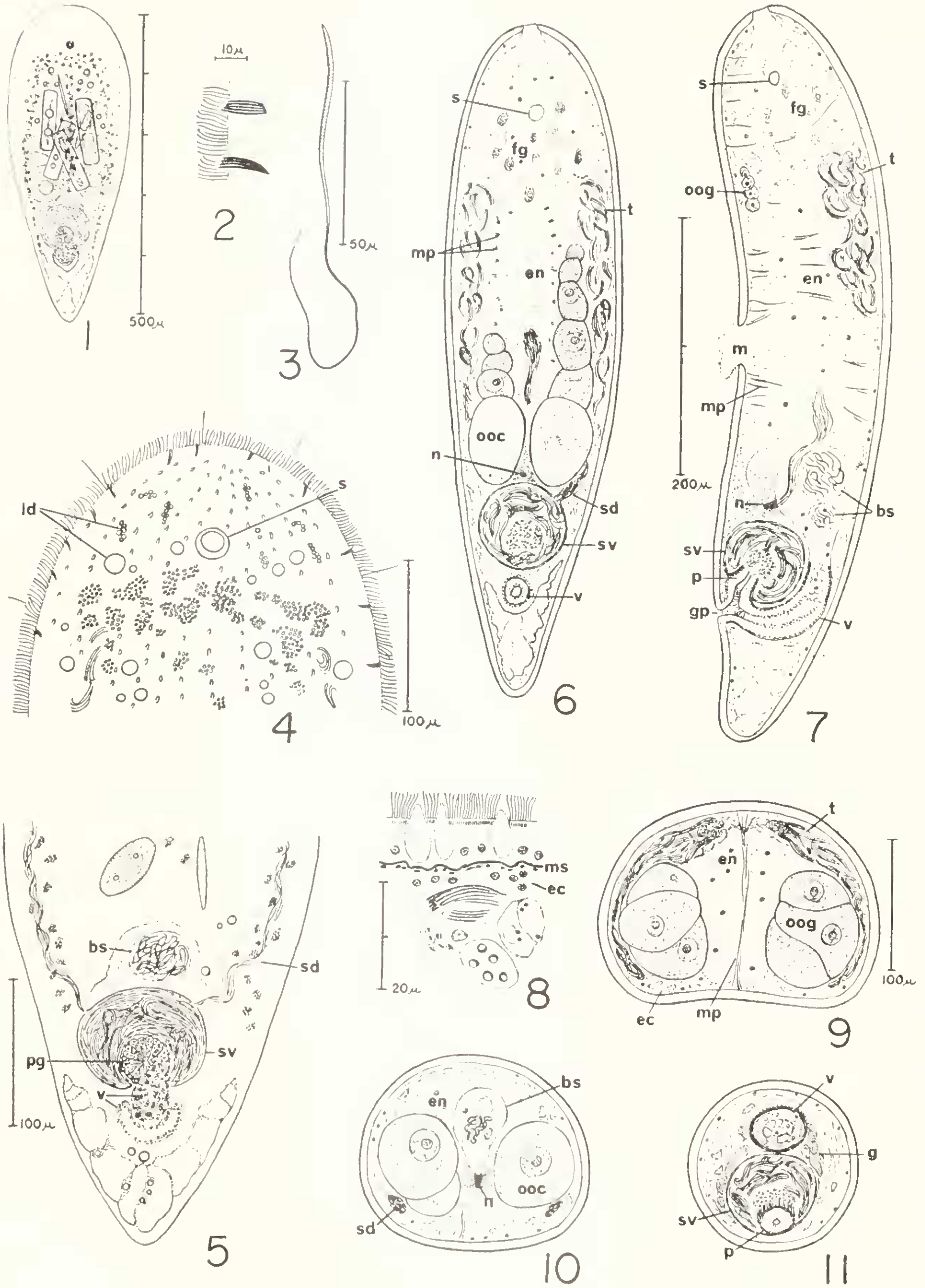

Plate I—*Parotocelis luteola*

All figures were prepared with the aid of a camera lucida, but in the case of specimens drawn from life (Figs. 1–5), most details were sketched in free-hand. Figures 6 to 11 are based together with rhabdocoels, alloeocoels, copepods, amphipods, and other small organisms.

My descriptions are based entirely on sexually mature specimens examined or fixed soon after collection. (Worms which are immature or which are not well nourished are unreliable.) The acoels were studied extensively in life, in both transmitted and reflected light. Gentle compression of the worms under a coverglass was usually necessary to make certain structures clearly visible. Addition of a small amount of a solution of magnesium chloride (approximately isotonic with sea water) to the drop of water in which the worms were swimming was generally helpful in narcotizing them in an extended condition without obviously affecting their appearance.

Stained whole-mount preparations were less useful than living acoels for morphological studies. However, a few whole-mounts of worms fixed in Bouin's fluid and stained with alum hematoxylin or borax carmine were prepared for permanent records.

The morphology of the acoels described in this paper was worked out largely by study of transverse, sagittal, and frontal serial sections (6 μ or 8 μ). The worms were fixed, usually after being narcotized, in Bouin's fluid or in a mixture of 90 ml. of a saturated aqueous solution of mercuric chloride with 10 ml. of formalin and 5 ml. of acetic acid, and then embedded in paraffin. Iron hematoxylin was used routinely for staining; sometimes the preparations were counterstained with eosin, orange G, or fast green FCF. A few series were stained with Harris' alum hematoxylin and eosin.

Descriptions of Species

Parotocelis luteola gen. nov., sp. nov.

Most of my material of this acoel was taken in shallow pools at the margins of a body of water known locally on San Juan Island as Argyle Lagoon (Lat. 48°

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on sections (6 μ) of specimens fixed in Bouin's fluid and stained with iron hematoxylin; certain details were supplied from adjacent sections in the same series.

Abbreviations for all figures: b, brain; bs, seminal bursa; ec, ectocytium; en, endocytium; fg, frontal glands; g, glands surrounding copulatory organs; ga, genital atrium; gp, genital pore; ld, lipid droplets; m, mouth; mp, parenchymal muscles; ms, subepicytial muscles; n, nozzle of seminal bursa; ooc, oocyte; oog, oogonium; p, penis; pg, granule-filled masses at tip of penis; s, statocyst; sd, sperm duct; sv, seminal vesicle; t, testis; v, vagina.

Figure 1. Specimen in contact with substrate; dorsal view.

Figure 2. Rhabdites at left margin of body.

Figure 3. Mature sperm.

Figure 4. Anterior end (specimen slightly compressed under coverglass); dorsal view.

Figure 5. Posterior end (specimen slightly compressed under coverglass); dorsal view. The anterior portion of the vagina, in which the lumen is obliterated by a syncytium containing refractile granules, obscures part of the seminal vesicle beneath it.

Figure 6. Frontal section. One of the oocytes is undergoing a maturation division.

Figure 7. Median sagittal section.

Figure 8. Epicytium, epicytial glands, subepicytial musculature, and portion of testis in transverse section just anterior to mouth.

Figure 9. Transverse section just anterior to mouth.

Figure 10. Transverse section through seminal bursa of same specimen.

Figure 11. Transverse section through penis, seminal vesicle, and anterior portion of vagina of same specimen.

31.3′ N.; Long. 123° 0.6′ W.).[1] The worms are usually abundant in muddy sand supporting a growth of *Enteromorpha*. *P. luteola* has also been collected in small numbers at Friday Harbor, among *Ulva and Enteromorpha* growing on a substrate of gravel mixed with muddy sand, at tide levels of about 0 to +2 ft.

When gliding actively, the length of *P. luteola* is typically about two and a half times the width (Fig. 1). The greatest width is usually near the end of the first one fifth of the body. The anterior end is broadly rounded; posteriorly, the body tapers rather gradually to a nearly acute tip. The largest specimens are about 700 μ in length and 230 μ in width, but they may become extended temporarily to a maximum length of about 840 μ and a width of about 180 μ. In worms which are in tight contact with the substrate, the thickness in the mid-dorsal region is usually about one-half the greatest width, so that the body appears definitely flattened. When swimming free, the worms become nearly cylindrical.

The statocyst (Fig. 4) lies about midway between the ventral surface and the dorsal surface, near the end of the first one-tenth of the body. In larger specimens, the diameter of the statocyst is about 20 μ, and that of the statolith is about 12 μ. Viewed on edge, the statolith is nearly hemispherical; the convex surface is uppermost.

In reflected light, the coloration of the body as a whole, excluding the digestive endocytium, is whitish, tinged faintly with orange; the orange color becomes more pronounced anterior to the statocyst. In most specimens which contain ingested diatoms, the endocytium is green, although in an occasional individual this region is brown or yellowish brown. In the area just behind the statocyst, there are small masses of a material which appears white in reflected light. Three discontinuous longitudinal streaks of this material extend for some distance posteriorly.

In strong transmitted light, the body is more or less translucent. In the endocytium, freshly-ingested diatoms with their characteristic olive-green, yellow-brown, or yellow-green color may be seen, together with those which have turned green or bluish green. Chlorophylls diffusing out of the diatoms undergoing digestion appear to be responsible for the green or blue-green color typically observed in this general area. In the ectocytium anterior to the statocyst, there is a crescentic band of yellowish-orange pigment; similar pigment is often found in small areas in the posterior part of the body, around the copulatory organs. Lipid droplets are scattered throughout the body. The larger of these, which may attain a diameter of about 20 μ, are yellow or orange; the smaller ones may be nearly colorless, yellow, orange, or bluish green, or some mixture of these colors. The lipid droplets apparently concentrate pigments which diffuse out of the diatoms. The material which is white in reflected light is seen to consist of granules or rods of a refractile substance. These granules form small aggregates (Fig. 4) within the ectocytium in the dorsal part of the body just behind the statocyst, and dorsal and dorsolateral to the endocytium. Under low magnification, the aggregates

[1] Argyle Lagoon is not natural. It was formed after an accumulation of gravel from a hillside excavation became deposited, together with sand and debris, on the seaward side of a small inlet of North Bay. At high tide, water may enter the lagoon through its narrow connection with the inlet. At low tide, some water drains out of the lagoon. However, the water level in the lagoon does not vary a great deal, and most of the time it is higher than that of North Bay and the inlet.

appear nearly black; under higher magnification, they appear brown. However, the individual bodies in the aggregates are nearly colorless.

The body is entirely covered by cilia about 10 μ long. Scattered over the body surface there are stiff, cilia-like bristles (Fig. 4) up to about 24 μ long. These are probably sensory in function. The bundles of epicytial rhabdites (Fig. 2) are rather evenly distributed on both the dorsal and the ventral surfaces. They fall into poorly-defined short rows (Fig. 4).

The mouth is located on the ventral surface, slightly anterior to the middle of the body. The pore is kept closed most of the time, but its position may be established by finding a characteristic convergence of rows of cilia. The mouth is capable of great distention during ingestion of food and during elimination of undigested material, such as diatom frustules.

The principal elements of the nervous system in this small acoel are not clear in any of my preparations. Close to the anterior end of the body, in front of the statocyst, a ring-like concentration of nerve tissue encircles the so-called "frontal organ" (the confluence of ducts of the frontal glands approaching the pore through which their secretion is discharged). However, the nerve tissue and ectocytium are so closely bound together that I have not established how many ganglia contribute to the brain mass, and I have not been able to trace any important nerves leading away from it.

Much of the anterior quarter of the body is occupied by the frontal glands and their secretion (Figs. 6, 7). In sections, the secretion is conspicuous as a pale yellowish material which is not appreciably stained by either hematoxylin or acid counterstains such as eosin, orange G, and fast green. The pore through which the secretion is discharged is circular and is located at the anterior tip of the body. The epicytium is supplied with numerous small glands (Fig. 8) within which the bundles of rhabdites are formed. The rhabdites are destroyed by the two fixatives which I used.

The subepicytial musculature (Fig. 8) consists of an outer layer of circular muscles and an inner layer of longitudinal muscles. In the parenchyma, there are scattered longitudinal and dorsoventral muscle fibers; dorsoventral muscles traversing the endocytium near the mouth are particularly conspicuous (Figs. 6, 7). The musculature associated with the copulatory organs will be described subsequently.

In the region of the mouth, the endocytium, into which food is ingested, occupies most of the body mass mesial to the ovaries and testes (Fig. 7). The endocytium extends anteriorly as far as the frontal gland cells and posteriorly as far as the anterior edge of the seminal vesicle. The ectocytial layer, which is very thin at the level of the mouth, becomes slightly more prominent anteriorly, and is very conspicuous in the posterior quarter of the body. Dorsal, lateral, and posterior to the copulatory organs, the vacuoles in the ectocytium reach a very large size (Figs. 1, 5, 6, 7).

The testis and ovary on each side of the body are closely apposed for most of their length. In the region just behind the frontal glands, the testes are lateral and dorsal to the string of small oogonia lying near the ventral epicytium (Figs. 6, 7). As the oogonia enlarge into oocytes, and therefore occupy progressively more of the body mass as they migrate posteriorly (Fig. 9), the testes become gradually restricted to a narrow zone lateral to the oocytes.

From the posterior end of each testis, a delicate duct carries sperm through the parenchyma to the seminal vesicle (Figs. 5, 10). The two sperm ducts enter the seminal vesicle at rather widely separated points on its anterolateral surfaces. The seminal vesicle (Figs. 5, 6, 7, 11) has a thin muscular wall, and in mature specimens invariably contains inactive sperm. Within the seminal vesicle, on its posteroventral side, there is a cluster of granule-filled masses which surround a small cavity continuous with the lumen of the penis. In life, the cluster resembles a group of cells (Fig. 5), but the boundaries of the individual masses are destroyed by fixation, and I have not been able to distinguish nuclei among the granules, which are refractile and are stained by hematoxylin. The penis appears to be of a type which is everted during copulation, and presumably when this takes place at least some of the granules at its tip are discharged.

The mature sperm (Fig. 3) of *P. luteola* are about 150 μ long. Behind the appreciably thickened anterior portion (slightly over one-third of the total length), the tail of the sperm narrows gradually to a very fine tip.

The vagina, supplied externally with an outer layer of longitudinal muscles and an inner layer of circular muscles, extends at first almost directly dorsally away from the genital atrium. This lower portion of the vagina has a distinct lumen (Figs. 6, 7); the lumen becomes gradually more extensive, and crescentic in outline as it is viewed from the dorsal side in living specimens (Fig. 5). The surface of the syncytial wall of the vagina next to the lumen is covered with small granules which appear to be of the same type as those associated with the tip of the penis. Some of these granules are noted within the tissue of the vagina and also within the lumen.

As the vagina arches anterodorsally over the seminal vesicle, the lumen becomes obliterated by a syncytial mass continuous with the syncytium of the rest of the vagina, and the layer of circular muscles becomes more pronounced. In life, the syncytium contains refractile crystal-like granules (Fig. 5); in specimens which have been fixed and sectioned, the granules are not preserved, and the syncytium is conspicuously vacuolated (Figs. 7, 11). Finally, the musculature disappears, and the vagina passes insensibly into a syncytium distinct from the digestive endocytium and within which the seminal bursa develops (Figs. 5, 7, 10). In some living specimens, as well as in sectioned preparations, sperm are observed in two or more spaces which may be connected or apparently separate (Fig. 7). Extending ventrally or posteroventrally from the bursa is a heavily cuticularized nozzle invested by what appears to be a fibrous tissue (Figs. 7, 10). The sperm in the seminal bursa usually exhibit considerable activity.

How the sperm reach the syncytium, within which the rather poorly-defined seminal bursa develops, is not clear. I have not been able to distinguish a continuous clear passage through the syncytium constituting that portion of the vagina which lies above the seminal receptacle. However, sperm have been noted in the lower portion of the vagina. It is possible that when insemination is effected, the sperm entering the vagina are simply forced through the syncytium to the region where the bursa is formed.

In the parenchyma around the seminal vesicle and anterior region of the vagina, there are a number of cellular elements which appear to be gland cells. The exact distribution of these glands and the pathways by which their secretion or secretions are delivered to other organs have not been worked out.

The holotype specimen, in the form of a set of serial sagittal sections, has been deposited in the United States National Museum (USNM No. 32902).

The nature of the brain of *P. luteola,* and the fact that its vagina enters the genital atrium behind the copulatory complex, indicate that it belongs in the family Otocelididae. Westblad (1948) established this family to include a single genus, *Otocelis,* which had previously been referred to the Convolutidae by most students concerned with this general group of acoels.

Westblad (1946) recognized only two species of *Otocelis: O. rubropunctata* (Schmidt) and *O. gullmarensis* Westblad. Ax (1959) pointed out that the acoel believed by Westblad to be *O. rubropunctata* is quite distinct from the worm described by Schmidt and later studied in detail by von Graff. The true *O. rubropunctata,* which has a single genital pore, is not definitely known to occur outside the Mediterranean Sea and Black Sea. Westblad's *O. "rubropunctata,"* from Scandinavian localities, has separate male and female pores. Ax proposed that it be called *O. westbladi.*

Two other acoels have rather recently been added to the genus *Octocelis. O. dichona* Marcus (1954) is distinctive in having the genital pore located at the posterior end of the body. *O. sachalinensis* Ivanov (1952) is probably more nearly similar to *O. rubropunctata* than to any other species of *Otocelis.* However, it lacks eyes, and the organization of the penis is very much like that in *P. luteola.* Certain of Ivanov's figures suggest that the tip of the penis of *O. sachalinensis* has masses of granules similar to those associated with the penis of *P. luteola,* although Ivanov did not mention any such masses in the text.

In the acoel I have described, the most distinctive feature, not shared by any of the other known species of *Otocelis,* is the peculiar nature of the anterior part of the vagina, where the lumen appears to be obliterated. It is primarily on the basis of this characteristic of *P. luteola* that I propose a new genus. I am fully aware that *O. sachalinensis* and *P. luteola* are similar in a number of respects, but the relationship of *P. luteola* to the genotype (*O. rubropunctata*) or to the other species of *Otocelis* is probably considerably more remote.

Raphidophallus actuosus gen. nov., sp. nov.

This acoel is moderately common in the small inlet of North Bay with which Argyle Lagoon communicates. Washings of *Ulva* detached from substrates of muddy sand or gravel at tide levels ranging from about −1 to +4 ft. often contain some *R. actuosus.*

When extended and gliding actively on a firm substrate (Fig. 12), the length of *R. actuosus* is equal to about four times the width. Anteriorly, the body is rounded; posteriorly, it tapers only slightly. The largest specimens, in a normal state of extension, are about 880 μ long and 220 μ wide. When the worms are in tight contact with the substrate, the ventral surface is flattened, but the thickness in the mid-dorsal region may nearly equal the width. When swimming free of the substrate, *R. actuosus* becomes almost cylindrical.

Of the three acoels described in this paper, *R. actuosus* is the most active, and it is also the most fragile. When the animal is swimming in contact with the substrate, its movements are jerky, and the posterior part of the body is often twitched back and forth, as if it were being irritated. Addition of a very little isotonic magnesium chloride may cause it to disintegrate, and when it is under slight pressure from a coverglass it is less likely to maintain its integrity than the other two species.

The statocyst is located near the end of the first one-eighth of the body. In larger specimens, its diameter is about 20 μ. The diameter of the statolith is about 14 μ. The shape of this structure is approximately hemispherical, and the convex surface is uppermost.

Viewed with reflected light, the body (except for the digestive endocytium) is whitish. The endocytium is typically brownish yellow, but it may be greenish yellow, or partly of this color. Deposits of bright white material are usually very conspicuous in the dorsal part of the body around the statocyst, and in a broken streak extending for most of the length of the body along the midline.

In strong transmitted light, the diatoms taken into the digestive endocytium are observed to change from a yellow-brown or olive color to greenish yellow and brownish yellow. The pigments diffuse out of the frustules and color the endocytium as a whole. Small lipid droplets are abundant in the ectocytial parenchyma, especially in the anterior half of the body. Most of these are yellow in color, and occur in clusters of various shapes; some clusters contain a large number of droplets, and are confluent with other clusters. The bright white deposits noted around the statocyst and along the midline when the worms are studied in reflected light are aggregates of small refractile granules which individually are pale yellowish green in color. The aggregates, however, appear blackish or brownish. They lie within the ectocytial parenchyma in the dorsal part of the body.

The body is entirely covered by cilia about 8 or 9 μ long. Scattered over the body surface are stiff, cilia-like bristles. Most of these are approximately 15 μ long, but in the caudal region some of the bristles may reach a length of nearly 30 μ.

The bundles of rhabdites of *R. actuosus* are conspicuous because they are closely spaced and are arranged in definite rows (Fig. 13). A particular row of rhabdites is never very long, however, and eventually merges with another row or terminates as two other rows converge.

The mouth is located on the ventral surface just posterior to the middle of the body. It is capable of rapid distention during the ingestion of food and elimination of undigestible residues (largely diatom frustules).

The brain appears to consist of four major ganglia, one anterolateral and one posterolateral to the statocyst on either side. Heavy commissures connect the ganglia in front of and behind the statocyst, so that the latter is almost completely enclosed within nerve tissue. My preparations do not clearly show the nerve trunks which originate from these ganglia.

The frontal glands and their accumulated secretion occupy a considerable part of the body mass in the vicinity of the statocyst (Fig. 17). The secretion appears in sectioned specimens as a pale yellowish material. The circular pore through which the secretion is discharged is located at the anterior end of the body, but is directed slightly downward. The epicytium is supplied with many small glands (Fig. 18) within which the bundles of rhabdites are formed.

The subepicytial musculature (Fig. 18) consists of an outer layer of circular muscles and an inner layer of longitudinal muscles. Parenchymal muscles are also present; these are most conspicuous in the anterior part of the body, in the region occupied by the frontal glands.

The digestive endocytium reaches anteriorly to the frontal glands and posteriorly nearly to the back edge of the seminal vesicle (Fig. 17). The ectocytial layer is rather thin in most regions of the body. It becomes appreciably thicker near the anterior end, but is most extensively developed in the posterior part of the body, where vacuoles within it are conspicuous lateral, dorsal, and posterior to the copulatory organs (Figs. 12, 15, 16, 17).

The testes and ovaries are approximately one-half the length of the body, and anteriorly they reach nearly to the level of the statocyst. In front of the mouth, the testes form a considerable part of the body mass. They are located above the string of enlarging oogonia, and their distribution is lateral and dorsal to the endocytium (Figs. 19, 20). For about one-half of their length, the testes of the right and left sides are confluent dorsally. However, as the endocytium becomes limited to the dorsal part of the body and the oocytes beneath it become very large, the testes become distinctly separate, and finally they occupy only a very small portion of the body mass as seen in transverse sections.

The genital pore (Figs. 15, 17) is located on the ventral surface near the beginning of the last quarter of the body. In living specimens, the genital atrium contains a number of more or less ovoid masses of granular material (Fig. 15). The source of these is not known. In sections of fixed specimens, the secretion within the genital atrium has the appearance of a vacuolated coagulum (Fig. 17); small granules which are stained by iron hematoxylin are scattered through this.

The seminal vesicle (Figs. 15, 16, 17, 21) is located posterodorsal to the genital atrium. The sperm ducts leading from the testes enter it at rather widely separated points on its anterolateral surface. The wall of the seminal vesicle is thin but muscular. The penis, as seen in sagittal sections (Fig. 17), arches from the genital atrium through the upper part of the seminal vesicle, and its lumen communicates with the cavity of the seminal vesicle at the rear. The penis is invested externally by an outer layer of longitudinal muscles and an inner layer of circular muscles, and its lumen is provided with a number of separate and very delicate cuticular rods. Presumably, the penis is everted during copulation. The cavity of the seminal vesicle is filled with inactive sperm. It is crescentic in outline when viewed from above, but it extends farther anteriorly near the ventral side of the seminal vesicle than near the dorsal side. Between the sperm mass and the penis there is a large accumulation of granules which are conspicuous in living specimens (Fig. 15) and which are stained strongly by hematoxylin (Figs. 16, 17, 21).

The mature sperm (Fig. 14) are about 110 μ long, and their structure is very interesting. Behind the thickened anterior region, a number of delicate cilia-like projections extend away from the sperm. The basal portions of these projections are appreciably thicker than the slightly longer outer portions. The posterior region of the sperm narrows gradually to a very fine tip.

The vagina (Fig. 17) extends anterodorsally from the genital atrium. It is short, and a part of it is ciliated. Where the lumen terminates, there are glands which produce the elongate clusters of granules often noted anterior to the genital pore in living specimens (Fig. 15). When worms of this species are compressed, the clusters of granules may actually protrude from the genital pore. In sectioned

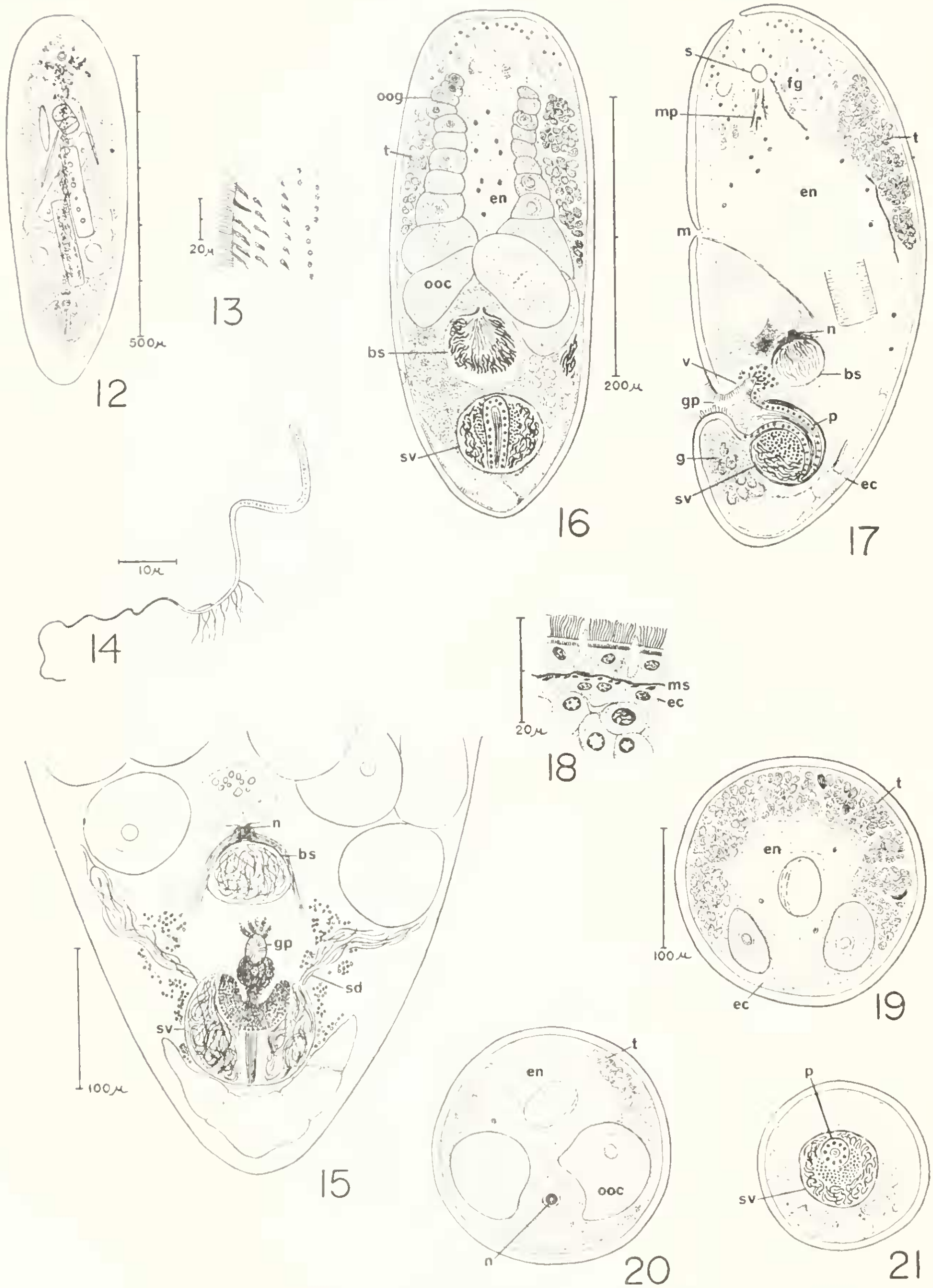

Plate II—*Raphidophallus actuosus*

All figures were prepared with the aid of a camera lucida, but in the case of specimens drawn from life (Figs. 12–15), most details were sketched in free-hand. Figures 16–21 are based on sections (6 μ) of specimens fixed in Bouin's fluid and stained with iron hematoxylin preparations, only traces of the clusters can be detected in the anteriormost part of the wall of the vagina, and a brownish-yellow coagulum is noted in the lumen of the vagina near them. Between the glandular cap of the vagina and the seminal bursa, there is a syncytial mass within which the nuclei are rather close together, and through which sperm are probably forced into the bursa at the time of insemination.

The holotype specimen, in the form of a set of serial frontal sections, has been deposited in the United States National Museum (USNM No. 32903). It was collected in the small inlet of North Bay which communicates with Argyle Lagoon, San Juan Island, Washington.

This acoel can be referred to the family Convolutidae, and may be rather closely related to certain of the diverse species of *Convoluta*. The penis lies within the seminal vesicle in much the same manner as that of *C. divae* Marcus (1950), *C. norvegica* Westblad (1946), and *C. flavibacillum* Jensen (see Westblad, 1946), but the presence of numerous cuticularized rods within the penis is distinctive. I base the genus *Raphidophallus* largely on this combination of characters.

Diatomovora amoena gen. nov., sp. nov.

This relatively large species is usually found in washings of *Ulva* growing on muddy sand or gravel in the small inlet of North Bay which communicates with Argyle Lagoon. Samples collected at tide levels ranging from −1 to +4 ft. generally contain *D. amoena;* as a rule, it is more abundant than *R. actuosus*. I have also found it in washings of *Ulva* and *Enteromorpha* taken from muddy sand in South Slough at Charleston, Oregon (Lat. 43° 20.4′ N.; Long. 124° 19.5′ W.) at tide levels of about +2 to +5 ft.

When extended and gliding in contact with a firm substrate (Fig. 22), the body is about four times as long as wide. The largest specimens are about 1200 μ by 300 μ. The body is rounded anteriorly and tapers slightly toward the posterior end. Although the body is usually widest near the middle, the width remains almost constant in the second and third quarters. The greatest thickness, just behind the middle of the body, is nearly equal to the width. When the worms are gliding on a firm substrate, the ventral surface is flattened; when swimming free, the body becomes nearly cylindrical.

(some preparations were counterstained with orange G); certain details were supplied from adjacent sections in the same series. For abbreviations, see legend for Figures 1–11.

FIGURE 12. Specimen in contact with substrate; dorsal view.

FIGURE 13. Rhabdites near left margin of body at the level of the statocyst.

FIGURE 14. Mature sperm.

FIGURE 15. Posterior end (specimen slightly compressed under a coverglass); ventral view. The masses of granular material shown next to the genital pore lie within the genital atrium.

FIGURE 16. Frontal section. In the anterior part of the body, the section shows the region slightly ventral to the level of the statocyst and pore of the frontal glands; one of the oocytes is undergoing a maturation division.

FIGURE 17. Median sagittal section.

FIGURE 18. Epicytium, epicytial glands, subepicytial musculature, and portion of testis in transverse section just anterior to mouth.

FIGURE 19. Transverse section just anterior to mouth.

FIGURE 20. Transverse section through nozzle of seminal bursa of same specimen.

FIGURE 21. Transverse section through seminal vesicle and penis of same specimen.

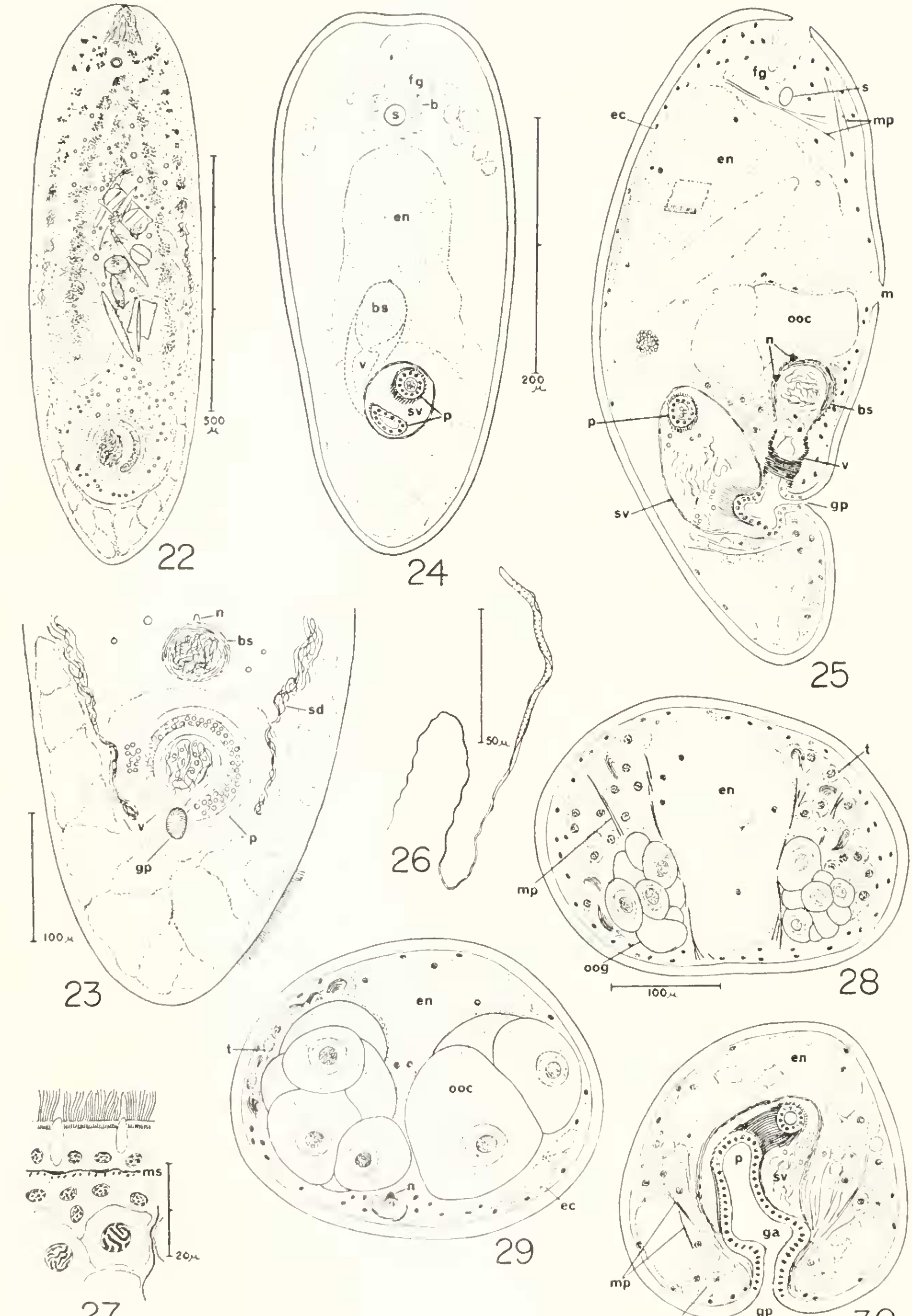

Plate III—*Diatomovora amoena*

All figures were prepared with the aid of a camera lucida, but in the case of specimens drawn from life (Figs. 22, 23, 26), most details were sketched in free-hand. Figures 24, 25, The statocyst lies near the end of the first one-tenth of the body. In larger individuals, its diameter is about 25 μ. The diameter of the hemispherical statolith is about 17 μ.

As viewed with reflected light, the body (excluding the digestive endocytium) is whitish, tinged with yellow; the yellow color, concentrated in lipid droplets, is prominent in the anterior quarter, and sometimes also near the posterior end. Near the dorsal surface, there are generally three discontinuous streaks of bright white material; these streaks originate behind the statocyst and diverge as they extend posteriorly. Some specimens have only one conspicuous streak along the midline; in others, the lateral streaks are distinct and the median streak is diffuse. The digestive endocytium is usually green, although sometimes it is greenish yellow.

In strong transmitted light, the ingested diatoms within the endocytium may be observed to turn from yellowish brown or yellowish green to a bluish green color. The endocytium as a whole is usually pale bluish green. Lipid droplets up to about 15 μ in diameter are scattered through the parenchyma, especially in the anterior quarter of the body. Some of these are quite yellow, and contribute to the yellowish cast noted in specimens examined in reflected light. The discontinuous streaks which appear white in reflected light are composed of greenish refractile granules (the larger of which are sculptured disks reaching a diameter of about 7 μ) concentrated in the ectocytium dorsal and dorsolateral to the endocytium. Under low magnification, the aggregates of these granules may appear blackish or brownish.

The body is covered by cilia about 10 μ long. The bundles of rhabdites resemble those of *R. actuosus;* they are closely spaced and are arranged in rather definite rows. Most of the rows are short and merge with other rows or simply terminate as the neighboring rows on either side converge toward one another.

The mouth is located on the ventral surface, just anterior to the middle of the body. It is capable of being considerably distended during the ingestion of food, which consists largely of diatoms and eggs of copepods, and during elimination of diatom frustules and other indigestible residues.

The nervous system has not been studied in detail. The brain appears to consist of four major ganglia and their commissures. There are two ganglia on either side of the statocyst—one anterolateral and the other posterolateral. These

27–30 are based on sections (6 μ) of specimens fixed in Bouin's fluid and stained with iron hematoxylin and orange G (or eosin); in most cases, some details have been supplied from adjacent sections in the same series. For abbreviations, see legend for Figures 1–11.

FIGURE 22. Mature specimen (slightly compressed under a coverglass); dorsal view.

FIGURE 23. Posterior end (specimen slightly compressed under a coverglass); ventral view. The globules on the topographic right side of the penis are within the lumen of the vagina.

FIGURE 24. Frontal section. Most details have been omitted, and the position of the vagina and seminal bursa, which lie some distance below the level of the structures traced, are rendered diagrammatically.

FIGURE 25. Median sagittal section. The vagina and seminal bursa were drawn from a number of sections considerably to the left of the section traced.

FIGURE 26. Mature sperm.

FIGURE 27. Epicytium, epicytial glands, subepicytial musculature, and portion of testis in transverse section just anterior to mouth.

FIGURE 28. Transverse section just anterior to mouth.

FIGURE 29. Transverse section through anterior nozzle of seminal bursa of same specimen.

FIGURE 30. Transverse section through region of genital pore and genital atrium of same specimen.

are fused almost completely, and communicate with their counterparts on the other side by thick commissures.

The frontal glands and their secretion (Figs. 24, 25) occupy much of the anterior fifth of the body. The pore through which the secretion is discharged is located at the anterior end of the body and is directed slightly downward. The glands within which the bundles of rhabdites are formed may be recognized within the epicytium (Fig. 27).

The subepicytial musculature (Fig. 27) consists of an outer layer of circular muscles and an inner layer of longitudinal muscles. Parenchymal muscles are also present. These are rather abundant in the region of the frontal glands (Fig. 25) and in the region of the copulatory organs (Fig. 30). However, parenchymal muscles having a nearly dorsoventral orientation are also prominent lateral to the endocytium near the mouth (Fig. 28).

In the region of the mouth, much of the body mass mesial to the testes and ovaries is occupied by the endocytial parenchyma into which food is ingested. The endocytium extends forward to the frontal glands (Fig. 25). Posteriorly it reaches beyond the anterior margin of the seminal vesicle, although it gradually becomes restricted to the dorsal part of the body mass, above the enlarging oocytes, seminal bursa, and seminal vesicle. The ectocytial parenchyma is rather thin where the endocytium is most extensive. It becomes appreciably better developed near the anterior end, and is very prominent in the posterior part of the body. Dorsal, lateral, and posterior to the copulatory organs, the ectocytium is characterized by large vacuoles (Figs. 22, 23, 24, 25, 30).

The testes are distinctly separate. In the region just behind the frontal glands, the testis on either side of the endocytium occupies nearly a third of the body mass. Farther posteriorly, however, the oogonia which are ventral to each testis become progressively larger, and the testes become gradually more restricted (Figs. 28, 29).

The genital pore (Figs. 23, 25, 30) is located on the ventral surface near the beginning of the last one-sixth of the body. The genital atrium has a ciliated epithelium and is externally lightly muscularized. The penis has a heavy external musculature consisting of an outer layer of longitudinal fibers and an inner layer of circular fibers. Its lumen is filled with globules which consist of small granules. In some preparations, these granules are stained distinctly by hematoxylin; as a rule, however, hematoxylin seems to be removed from them by routine destaining, and they become readily colored by eosin and orange G.

The penis leaves the left side of the genital atrium and follows a nearly circular ascending path through the seminal vesicle. The cavity of the seminal vesicle is filled with inactive sperm and globules of the type observed within the lumen of the penis. The delicate sperm ducts passing posteromedially from the testes enter the seminal vesicle on its dorsolateral surfaces.

The mature sperm (Fig. 26) are approximately 250 μ long. From the thickened anterior portion, the body becomes gradually narrowed to a very fine tip. A conspicuous undulating membrane spirals around the anterior two-thirds of the sperm. Undulations of the more slender posterior region appear to be continuous with those of the undulating membrane, and perhaps the latter extends almost the entire length of the sperm.

The vagina (Figs. 24, 25) has a thick tunic of circular muscles, and leaves the genital atrium ventral to the seminal vesicle. It is directed at first slightly to the right, then bends toward the midline on its course to the seminal bursa. For most of the length of the vagina, the lumen is distinct, and this may contain a number of globules of the type noted within the seminal vesicle and penis. Just before the vagina reaches the bursa, the lumen is obliterated by a syncytial mass continuous with the syncytial wall of the vagina. In life, this mass often contains clusters of refractile granules, and is very similar to that which obliterates the lumen of the anterior part of the vagina in *P. luteola.* In fixed and sectioned specimens, it is vacuolated and the granules are not preserved. The seminal bursa is invested by a heavy coat of fibrous elements; external to this, there are some widely-spaced muscles.

The bursa has two cuticularized nozzles (Fig. 25); one of these is directed almost anteriorly, and the other is usually directed dorsally or anterodorsally. The bursa generally contains active sperm, but in some specimens it is filled with the granule-bearing syncytium which usually characterizes the anterior portion of the vagina. It appears likely that unless the bursa is distended by sperm forced into it at the time of insemination, it tends to collapse and thus appears to envelop the syncytial mass just behind it.

Gland cells are extensively developed in the parenchyma around the copulatory organs, but I have not worked out the pathways by which the secretion or secretions of these glands are delivered to other structures.

The holotype specimen, in the form of a set of serial sagittal sections, has been deposited in the United States National Museum (USNM No. 32904). It was collected in the inlet of North Bay which communicates with Argyle Lagoon, San Juan Island, Washington.

Like the preceding species, this acoel belongs in the Convolutidae. Its long and highly muscular penis is somewhat similar to that of *Aphanostoma macrospiriferum* Westblad (1946) and *A. rhomboides* (Jensen) (see Westblad, 1946). However, neither of these species has a seminal bursa. When a bursa is present in members of the genus *Aphanostoma,* it does not have a cuticularized nozzle, although Westblad has questioned the importance of this characteristic in setting *Aphanostoma* apart from *Convoluta.* The heavily muscularized vagina of *D. amoena* and the nature of its seminal bursa, which has two nozzles and a thick wall consisting of fibrous elements surrounded by muscles, are characteristics which have persuaded me to propose a new genus.

Summary

Acoels belonging to three new genera are described. *Parotocelis luteola* is referred to the family Otocelididae. *Raphidophallus actuosus* and *Diatomovora amoena* are placed in the family Convolutidae. All of these acoels have been collected intertidally on San Juan Island, Washington, on substrates of muddy sand and gravel supporting growths of *Ulva* and *Enteromorpha. D. amoena* has also been found at Charleston, Coos County, Oregon.

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